

FEEDING RATES AND FOOD CONVERSION EFFICIENCIES IN THE APPLE SNAIL *POMACEA CANALICULATA* (CAENOCASTROPODA: AMPULLARIIDAE)

Nicolás E. Tamburi & Pablo R. Martín*

*Universidad Nacional del Sur, Departamento de Biología, Bioquímica y Farmacia,
San Juan 670, 8000 Bahía Blanca, Argentina*

ABSTRACT

Pomacea canaliculata is the only freshwater snail listed as one of the 100 worst invaders worldwide. Recent studies have demonstrated that small *Pomacea* snails have higher foraging and competitive abilities than larger snails and hence that ecological and agricultural damage of this invasive snail may be size-dependent. Furthermore, females of *P. canaliculata* usually reach larger sizes than males, a pattern that results from higher growth rates and not from higher survivorship in females; however, the proximal causes of the sexual dimorphic growth rates are unknown. In this study, we investigate the ingestion rates and growth efficiencies of *P. canaliculata* in order to explain the ontogenetic and sexual differences in growth and food consumption patterns. Two experiments were performed to study specific ingestion rates and the efficiency in food conversion to body mass at different feeding conditions. Ontogenetic and sexual differences were found in the specific ingestion rates. These decreased inversely with shell length and were higher for females than for males of comparable size. Conversion efficiencies decreased with age in both sexes, in males noticeably earlier than in females. Under high food availability conditions, the decrease is sharper than under low food availability. However, the effect of food availability almost disappeared when in the effect of size was removed. The sexual dimorphism of growth efficiencies and ingestion rates explain why females tend to reach a larger adult size than males, a pattern probably explained by development of the testicle and correlated reduction of mid-gut gland size. Our results on ontogenetic patterns of ingestion rates support predictions that during the reproductive season small snails may cause a great part of the damage to aquatic crops and natural wetlands.

Key words: growth, sexual dimorphism, allometry, invader, agricultural damage.

INTRODUCTION

Pomacea canaliculata (Lamarck, 1822) is native to South America and has been introduced in Asia, North America, and Hawaii for aquaculture and aquarium trade (Cowie et al., 2006; Rawlings et al., 2007; Hayes et al., 2008), where they have become established as serious pests of aquatic crops (Joshi & Sebastian, 2006). In addition, they are able produce major environmental changes resulting from the depletion of aquatic plants (Carlsson et al., 2004). *Pomacea canaliculata* has been listed as one of the 100 worst invaders worldwide and has the distinction of being the only freshwater snail on that list (Lowe et al., 2000). High growth and reproductive rates, polyphagous feeding habits, amphibious respiration, and aestivating capacity (Cowie, 2002; Estebenet & Martín,

2002) make *Pomacea* species highly adaptable and resistant to diverse environmental conditions, probably explaining in part both their pest status and the interest they attract as aquaculture organisms (e.g., Mendoza et al., 1999; Ramnarine, 2004).

Most research has focused recently on applied aspects of its biology and ecology (e.g., Tanaka et al., 1999; Carlsson et al., 2004; Yusa et al., 2006; Peña & Pocsidio, 2007), but some fundamental aspects of its basic biology remain obscure. Females of *P. canaliculata* reach larger sizes than males, both in natural habitats and when reared in the laboratory, a pattern that results from higher growth rates rather than from different survivorship rates (Martín & Estebenet, 2002; Estebenet et al., 2006). *Pomacea canaliculata* females always mature at an older age than males, indepen-

*Corresponding author: pmartin@criba.edu.ar

dently of food availability (Estoy et al., 2002; Tamburi & Martín, 2009). In animals with asymptotic growth after maturity, the sex that matures later is usually the larger one (Stamps & Krishnan, 1997). However, the asynchronic maturity does not fully explain the sexual size dimorphism, because *P. canaliculata* are often dimorphic long before maturity (Estebenet & Martín, 2003). In spite of the generality of this pattern in this species, and its occurrence in other apple snails (Estebenet et al., 2006), the proximal causes of the dimorphic growth rates are still unknown. Higher ingestion rates or more efficient use of food by females appear to be the most plausible explanations.

Higher ingestion rates for juvenile snails in relation to those of adults have been reported for *P. canaliculata* and *Pomacea insularum* (d'Orbigny, 1835) (Boland et al., 2008) and for the Indian apple snail *Pila globosa* (Swainson, 1822) (Hannifa, 1982). In field experimental enclosures with *P. canaliculata*, Carlsson & Brönmark (2006) demonstrated that small snails have higher foraging and competitive abilities than big snails, indicating that the degree of damage from this invasive snail to aquatic vegetation or crops may be size-dependent. Knowledge of size-dependent feeding rates may be useful for predicting damage to aquatic cultures and in developing food-efficient feeding regimes for apple snail aquaculture programs (Mendoza et al., 1999; Ramnarine, 2004).

In this study, we investigate the ingestion rates and growth efficiencies of *P. canaliculata* under different food availability conditions, with the goal of determining if these variables explain the ontogenetic and sexual differences in growth and resource consumption patterns reported for this apple snail.

MATERIALS AND METHODS

Source of Snails and General Rearing Conditions

The original source of all the snails used in this study was a population from the Curamalal stream (southern Buenos Aires Province, Argentina), which has been the subject of previous studies (Martín & Estebenet, 2002; Estebenet & Martín, 2003). All experiments were performed in a rearing chamber at $25 \pm 3^\circ\text{C}$ and a 14:10 h (light:dark) photoperiod. Snails were reared in tap water saturated with CO_3Ca and fed on fresh lettuce only.

Experiment 1: Ingestion Rates

The snails used to determine the daily ingestion rates were obtained from laboratory stocks (originated from field collected egg-masses) and supplemented with field-collected snails that had been maintained in laboratory conditions for at least a week. They were all fed *ad libitum* during three days before the beginning of the trials. Snails were carefully observed to detect the testicle through the translucent shell (Takeda, 1999) and the humping of the operculum in males (Estebenet et al., 2006). These traits were clearly noticeable in males whose shell was longer than 15 mm, so that smaller snails were categorized as undifferentiated and bigger ones, lacking male traits, as females. The same method was used in Experiment 2, where all the snails were correctly sexed (confirmed by oviposition in females and by the copulation behavior in males; Tamburi & Martín, 2009).

To estimate food ingestion relative to size, snails with shell lengths from 5 to 55 mm were maintained with weighed surplus lettuce in a rearing chamber for 24 hours to account for daily rhythm in activity and feeding (Heiler et al., 2008). Fresh hydrated lettuce, drained by gentle centrifugation, was weighed with an analytical scale at the start and at the end of the experiment to quantify the amount consumed. Shell length (SL, mm), from the apex to the lower margin of the peristome (Estebenet & Martín, 2003), was measured for each snail with a caliper (for snails larger than 10 mm) or under a stereoscopic microscope with micrometric lens. With the aim that the total weight of lettuce consumed was in agreement with the precision of the scale (0.1 mg), the consumption of snails larger than 15 mm was estimated individually, while 19 sets of 2 to 15 individuals of similar size (maximum CV% for shell length = 6.3) were used for smaller ones. To avoid feeding interference among individuals, the volume of the aquaria and the amount of lettuce were well in excess relative to the whole mass of snails and their consumption. Live snail weight (LW, g) was obtained individually or for the set of snails of each feeding trial, respectively (after allowing the snails to crawl over a plastic surface for a few minutes to release the water retained in the pallial cavity). To account for hydration effects, the lettuce consumed was corrected by a factor obtained from the weight gain of similar amounts of lettuce in four control aquaria without snails.

The specific ingestion rate (SIR, d^{-1}) was calculated as the lettuce consumed (LC, g) per day relative to the snail live weight (LW, g). After a log-log transformation to linearize the relationship (i.e., $\log_{10} \text{SIR} = \log_{10} a + b \cdot \log_{10} \text{SL}$), a least squares regression was performed to obtain a simple allometric equation ($\text{SIR} = a \cdot \text{SL}^b$) for SIR relative to shell length (SL, mm). For the SIR-SL regression, the mean shell length and the pooled live weight of, and the lettuce consumed by, the set of snails in each feeding aquarium were employed, whereas for snails bigger than 15 mm the individual values of these variables were used. In order to allow comparisons with previous studies and to standardize food availability in growth efficiency experiments, similar allometric models were built for LC-LW and for LC-SL.

Experiment 2: Growth Efficiencies

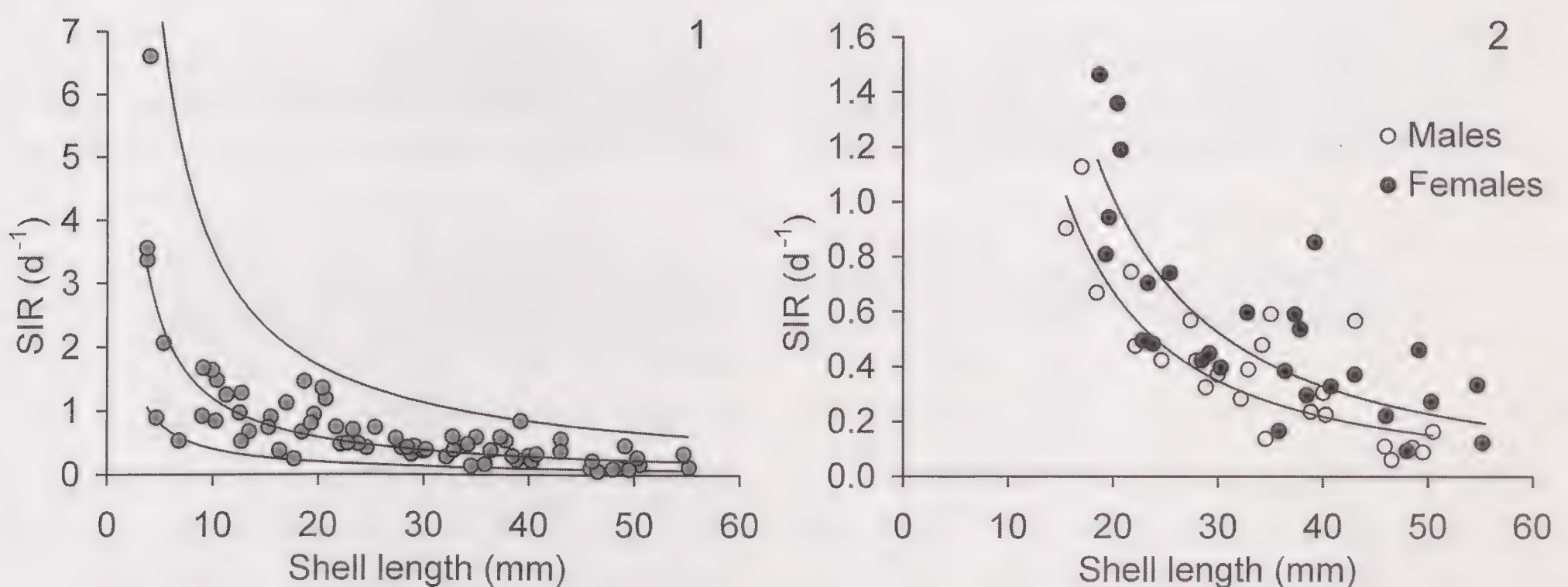
In this experiment, the efficiency of conversion of food to body mass was analyzed under different levels of relative food availability. The whole experiment lasted 70 weeks, and the main goal was to study the reaction norm of age and size at maturity to food availability (Tamburi & Martin, 2009), but here mostly pre-reproductive data were considered. No death was recorded during the experimental period.

Hatchlings from a single egg mass laid by a laboratory female that had been coupled during all her life with the same male, were reared during three weeks in a 20 l aquarium. Seventy two of these full-sib snails were then randomly selected (shell length: $4.96 \text{ mm} \pm 0.056$, mean

$\pm \text{SE}$, $n = 25$), and thereafter reared in isolation in 3 l aquaria under seven levels of relative food availability (FA%: 100, 87, 73, 60, 47, 33 and 20%). The expected daily amount of drained fresh lettuce ingestion by a snail of a given size (FA100%, g) was calculated using the LC-SL equation obtained from the data of Experiment 1 (i.e., $\text{LC} = \text{FA100\%} = 0.0033 \cdot \text{SL}^{1.9322}$, $R^2 = 0.86$, $n = 70$).

Each Monday water was changed, aquaria were cleaned and their position within the rearing chamber was randomly changed. Snails were carefully observed to try to detect their sex as early as possible, and the shell length (SL) of each snail was measured as described in Experiment 1 (using a micrometric lens up to the sixth week of the experiment or with a caliper afterwards). The weekly amount of lettuce for each FA% level was calculated according to the mean shell length of males and females assigned to it, provided in two half-doses on Tuesdays and Fridays. On Mondays, the snails were not fed because this day was reserved in the experimental schedule for coupling with mature snails (reared independently for the maturity study). From the sixth week onwards, the live weight (LW, g) of each snail was measured at four or five weeks intervals.

To investigate the growth efficiencies at the same age, food conversion efficiencies (FCE) were calculated as $\text{FCE}_{i,f} = (\text{LW}_f - \text{LW}_i) \cdot \text{AF}_{i,f}^{-1}$, where LW_i and LW_f are live weights at i th and f th week and $\text{AF}_{i,f}$ (g) is the accumulated weight of lettuce consumed in the same period. Except in the case of some males of the FA100% level during some weeks, the offered ration was to-



FIGS. 1, 2. Scatter-plots of specific ingestion rate (SIR) vs. shell length in *P. canaliculata* (curves were generated through the appropriate simple allometric models). FIG. 1: All snails (outer curves represent 95% prediction intervals); FIG. 2: Only differentiated snails.

TABLE 1: Two-way ANOVAs for food conversion efficiency (FCE) in *P. canaliculata* with sex and food availability (FA%) as main factors, calculated for the 0–6, 6–10, 10–14 and 14–19 weeks intervals (#: one-way ANOVAs for females only).

FCE	Sex	FA%	Sex x FA%
0–6	$F_{1, 55} = 0.439$ $p = 0.511$	$F_{6, 55} = 2.300$ $p = 0.047$	$F_{6, 55} = 0.527$ $p = 0.785$
6–10	$F_{1, 55} = 13.000$ $p < 0.001$	$F_{6, 55} = 52.860$ $p < 0.001$	$F_{6, 55} = 5.287$ $p < 0.001$
10–14 #	-	$F_{4, 21} = 7.419$ $p < 0.001$	-
14–19 #	-	$F_{4, 19} = 20.360$ $p < 0.001$	-

tally consumed, so AF_{if} was calculated as the sum of offered rations.

To investigate the growth efficiencies independently of size, the accumulated amount of food consumed to reach a given shell length (AFC, g) was calculated at 1mm intervals for shell lengths between 13 and 22 mm. For each snail, the moment at which a given shell length is attained (ASL, mm) was obtained by lineal interpolation between shell lengths at two successive weeks. The amount of food consumed since the previous Monday was also obtained by linear interpolation and added to the accumulated amount consumed up to the previous week.

The effect of food availability and sex on FCE and LW was investigated through two-way ANOVAs. Levene’s test for homogeneity of variances was not rejected for FCE, while a

Log_{10} transformation was required for LW. AFC was explored through a repeated measures ANOVA, with sex and FA% as main factors and the attained shell length (ASL) as the repeated measure or within-subject factor. Due to a significant non-sphericity (Mauchly’s W test), the degrees of freedom were corrected by Greenhouse-Geisser’s Epsilon.

RESULTS

Experiment 1: Ingestion Rates

No significant differences among males, females and undifferentiated snails were found in the rate at which the specific ingestion rate (SIR) decreased with shell length (slope equality test: $F_{2, 65} = 1.65$, $P > 0.199$). For the whole sample

TABLE 2: Two-way ANOVA for the amount of food consumed (AFC) in *P. canaliculata* with sex and food availability (FA%) as main factors and attained shell length (ASL, from 13 to 22 mm) as repeated measure.

	Source	SS	df	F	p
Within-subject	ASL	9415.2	9	2735.2	< 0.001
	ASL x Sex	66.704	9	19.378	< 0.001
	ASL x FA%	29.535	54	1.430	0.182
	ASL x Sex x FA%	31.863	54	1.543	0.139
	Error (ASL)	182.44	477		
Between-subject	Sex	45.827	1	6.267	0.015
	FA%	45.142	6	1.029	0.417
	Sex x FA%	35.565	6	0.811	0.566
	Error	378.54	53		

TABLE 3: One-way ANOVA for the amount of food consumed (AFC) in males of *P. canaliculata* with food availability (FA%) as main factor and attained shell length (ASL, from 13 to 22 mm) as repeated measure.

Source		SS	df	F	p
Within-subject	ASL	5996.8	9	1296.9	< 0.001
	ASL x FA%	28.710	54	1.035	0.430
	Error (ASL)	129.47	252		
Between-subject	FA%	62.970	6	1.050	0.415
	Error	279.58	28		

of snails (Fig. 1), the SIR was inversely related to shell length ($b = -1.029$; CI95% limits: -1.21 and -0.84); snails 12 mm-long consumed their own live weight in lettuce by day while for snails 50 mm-long the daily consumption was only 20% of their weight. The allometric coefficients for lettuce consumed (LC) per day relative to live weight or shell length were $b = 0.651$ (CI95% limits 0.59 and 0.71; $R^2 = 0.857$) and $b = 1.932$ (CI95% limits: 1.74 and 2.12; $R^2 = 0.862$), respectively. For SIR, significant differences in elevation were detected between sexes (elevation equality test: $F_{1, 49} = 9.94$, $P < 0.003$), ingestion rates being 50% higher for females than for males of the same shell length (Fig. 2) (back-transformed adjusted means for a 32.3 mm-long snail: 0.462 d⁻¹ and 0.312 d⁻¹, respectively).

Experiment 2: Growth Efficiencies

The food conversion efficiency during the first six weeks (FCE₀₋₆) showed only a marginally significant effect of food availability (Fig. 3, Table 1). During the following period, the FCE₆₋₁₀ showed a significantly different effect of food availability in each sex (Fig. 4, Table 1): no difference appeared between females fed at

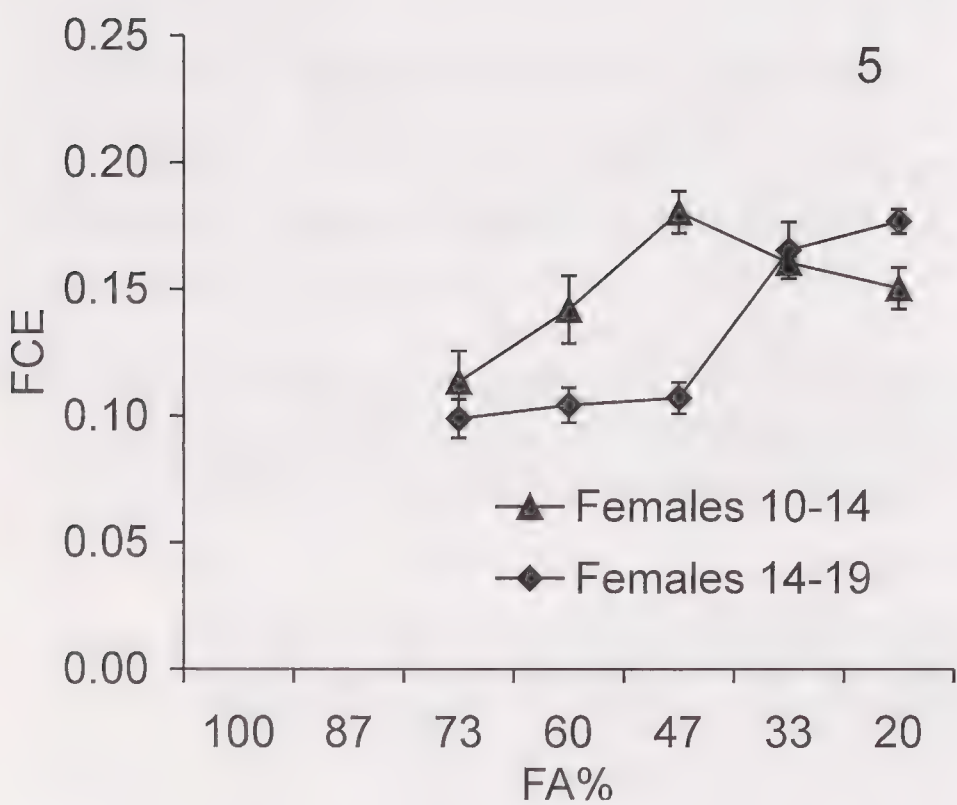
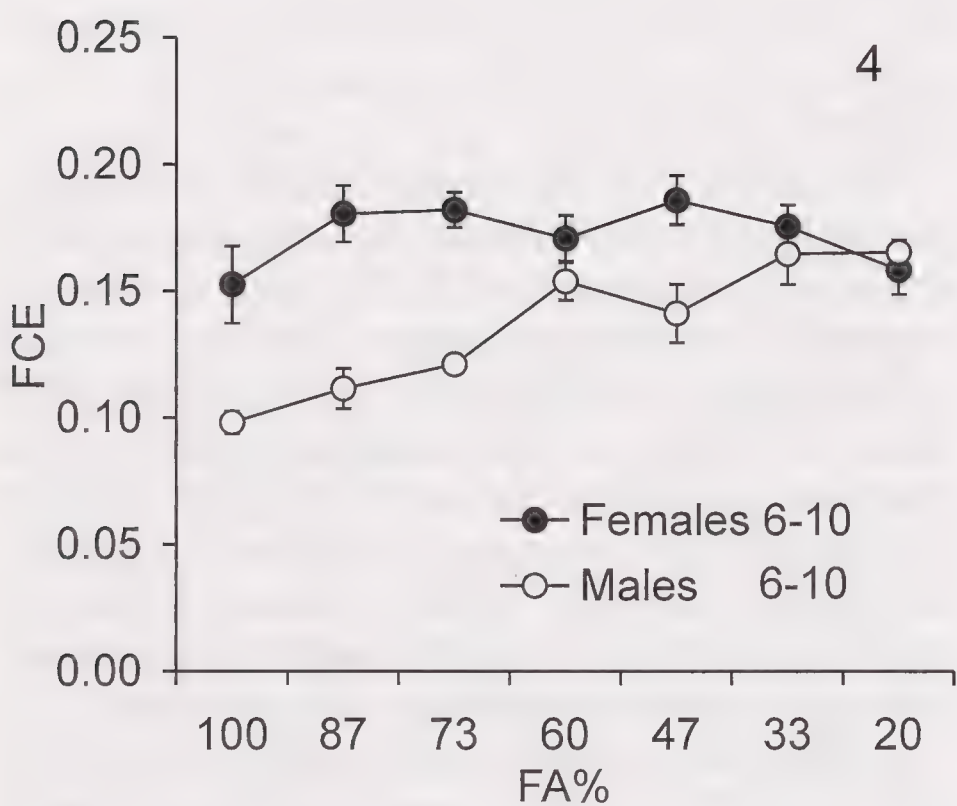
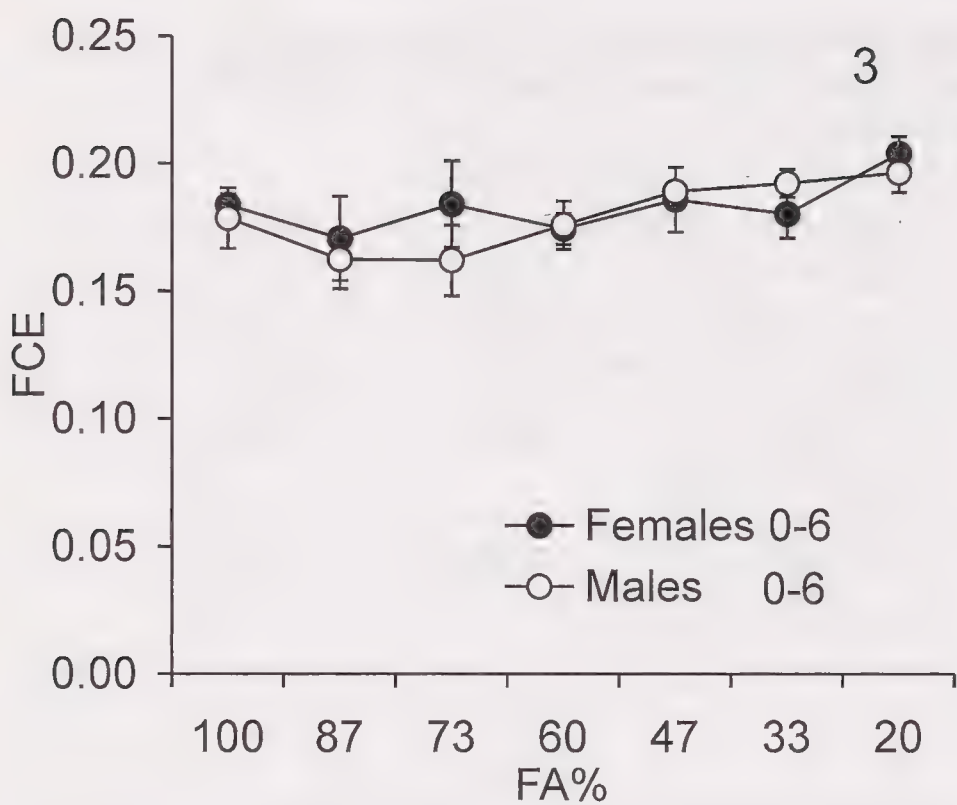
different FA% (one-way ANOVA: $F_{6, 27} = 1.51$, $p = 0.213$), while in males the FCE decreased significantly with FA% (one-way ANOVA: $F_{6, 28} = 11.31$, $p < 0.001$).

The males of all FA% levels and all the females from the 100 and 87 FA% levels were already mature by week 14 so FCEs were compared during the following two periods for the immature females of the remaining FA% levels. The FCE of these females was significantly affected by food availability, although a monotonically decreasing trend with FA% was apparent only at 14 to 19 weeks (Fig. 5, Table 1). For the same treatment and sex, the FCE values showed a general decreasing trend throughout the experiment.

Differences in size among the snails of the different FA% levels were early noticeable in the experiment. The snails' weight ($\log_{10} LW$) at the sixth week was significantly affected by food availability ($F_{6, 55} = 293.81$, $p < 0.01$) but no inter-sex differences were found ($F_{1, 55} = 0.457$, $p = 0.502$; FA% x sex: $F_{6, 55} = 0.567$, $p = 0.754$). By the tenth week, a significant effect of the sex of snails ($F_{1, 55} = 62.08$, $p < 0.01$) appeared on the already significant effect of food availability ($F_{6, 55} = 892.47$, $p < 0.01$), being stronger in treatments of higher FA% (FA%

TABLE 4: One-way ANOVA for the amount of food consumed (AFC) in females of *P. canaliculata* with food availability (FA%) as main factor and attained shell length (ASL, from 13 to 22 mm) as repeated measure.

Source		SS	df	F	p
Within-subject	ASL	3686.05	9	1739.64	< 0.001
	ASL x FA%	34.150	54	2.686	0.009
	Error (ASL)	52.970	225		
Between-subject	FA%	26.910	6	1.039	0.424
	Error	107.95	25		



FIGS. 3–5. Food conversion efficiency (FCE, mean $\pm$ SE) for pre-reproductive males and females of *P. canaliculata* under different food availabilities (FA%). FIG. 3: 0th to 6th week interval; FIG. 4: 6th to 10th week interval; FIG. 5: 10th to 14th and 14th to 19th week intervals (only for females that have not commenced egg laying).

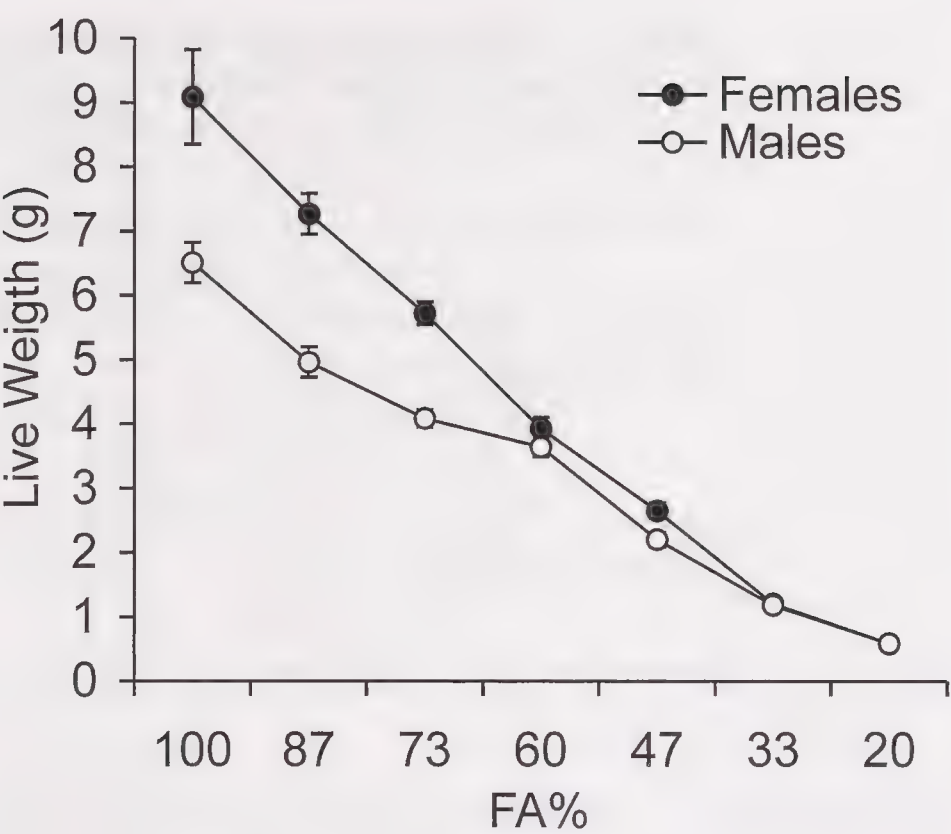
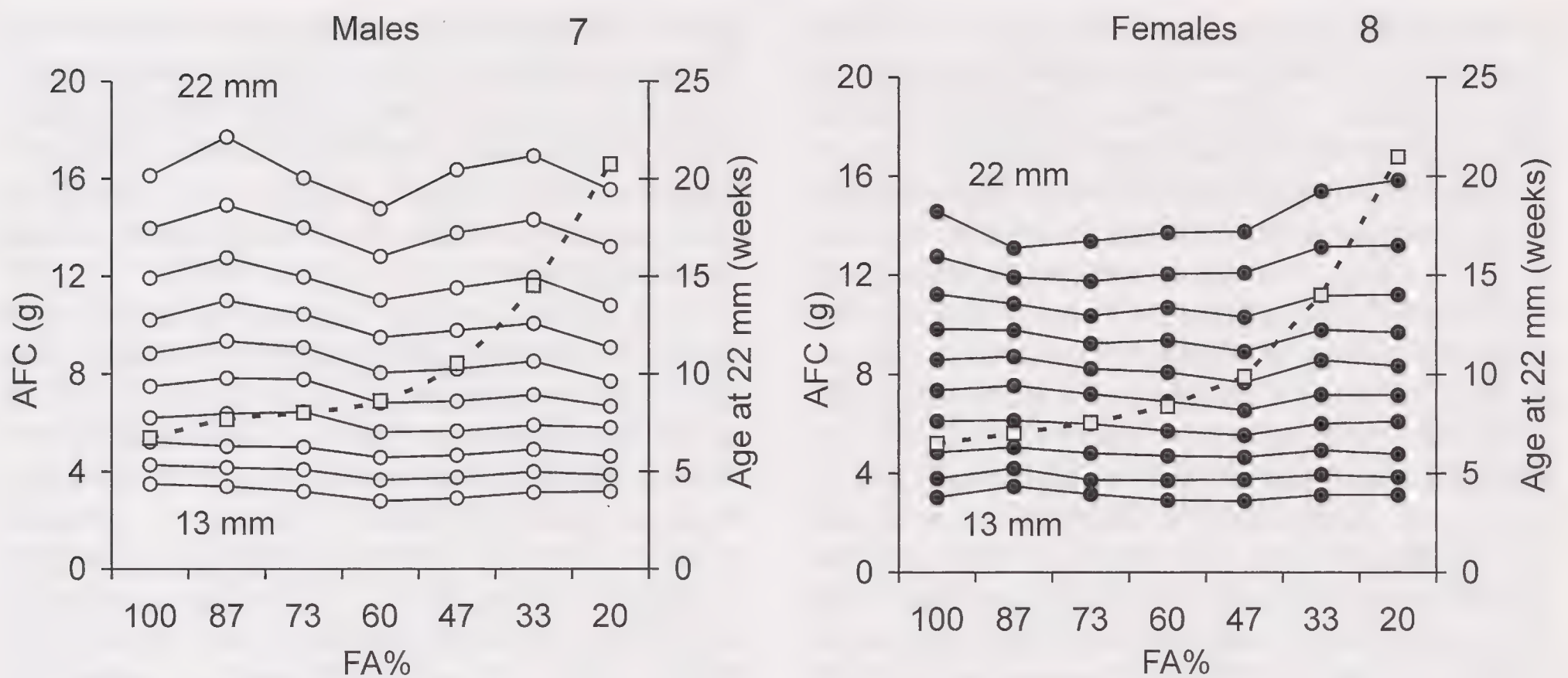


FIG. 6. Live weight (LW, mean $\pm$ SE) for both sexes of *P. canaliculata* at 10th week of rearing under different food availabilities (FA%).

x sex: $F_{6, 55} = 6.59$, $p < 0.01$); females were increasingly heavier than males as food availability increased (Fig. 6). These same trends continued as long as the experiment ran and were also very similar when shell length was considered as an indicator of size.

A preliminary within-subject analysis using the whole data set of the amount of food consumed to attain a certain size (AFC) showed a significant effect of shell length and a significant interaction between shell length and sex (Table 2); the interaction between shell length and FA% and the second order interaction (ASL x FA% x sex) were both non-significant. The between-subject analysis of the same data set detected only a significant effect of sex (Table 2), with males requiring an increasingly higher amount of food than females to attain a certain size (Figs. 7, 8). Consequently, the analysis was split by sex to investigate in detail the effect of FA%.

The within-subject analysis for males showed only a significant effect of shell length while the between-subject analysis detected no differences between the FA% levels in the amount of food required to attain a given size (Fig. 7, Table 3). The same analyses for females showed a significant effect of shell length but also a significant interaction with the FA% levels that probably masked the differences among FA% levels in the between-subject analysis (Table 4); a noticeable effect of food availability on AFC appeared only in the late measurements of the



FIGS. 7, 8. Amount of food consumed (AFC) to attain a given shell length (entire lines, from 13 to 22 mm at 1 mm intervals) for *P. canaliculata* snails under different food availabilities (FA%; white squares represent the mean age of each FA% level when a shell length of 22 mm was attained). FIG. 7: Males; FIG. 8: Females.

lowest FA% (Fig. 8). The time required to attain a certain size (i.e., 22 mm) increased more than three fold with a decrease of 80% in trophic availability; males from the FA% levels of 20 and 33% were the only ones already showing copulatory behavior at this size, after attaining shell lengths of 15 and 17 mm, respectively.

DISCUSSION

Both ontogenetic and sexual differences were found in the specific ingestion rates of *Pomacea canaliculata* snails; this rate decreased inversely with shell length and was higher for females than for males of comparable size. Conversion efficiencies decreased with age in both sexes, the decrease being noticeable earlier in males than in females and greater at high than at low food availability levels; however, the effect of food availability almost disappeared when the effect of size was removed.

The specific ingestion rate decreases with shell length, from hatchlings to adult snails, when they are maintained under *ad libitum* palatable food. According to allometric models of herbivore feeding (Belovsky et al., 1999), which assume simple scaling growth, the food intake per unit time (C) would increase relative to body mass (M) with an allometry coefficient $b = 0.66$, and in turn body mass would increase to the cube of body length ($b = 3$). Therefore the

allometry coefficient for the specific ingestion rate ($SIR = C/M$) relative to body length would be $b = -1$. In our study, the SIR was inversely related to shell length ($b = -1.029$), suggesting that a limitation in the specific ingestion rate arises as a result of the quadratic increase in the cross section of the digestive tube relative to the cubic increase in the individual biomass that it must serve. Allometric limitations of this kind seem common in apple snails, perhaps owing to shared ontogenetic patterns. Higher specific ingestion rates for small snails relative to big ones have been recently reported for *P. canaliculata* and *P. insularum* feeding on different plant species (including lettuce, Boland et al., 2008; Burlakova et al., 2009). In the Indian apple snail *Pila globosa*, specific feeding rates on *Ceratophyllum demersum* also decreased with size independent of food availability (Hannifa, 1982). Weight specific oxygen consumption rates (Freiburg & Hazelwood, 1977; Santos et al., 1987) also decrease with weight in *Pomacea* spp.; this could be in turn related to allometric limitations in gas exchange surfaces, an energy intake limited by size or probably both simultaneously. These allometric effects can explain in part the asymptotic decrease in growth rates in *P. canaliculata* (Estebenet & Martín, 2002).

Allometry coefficients for ingestion rates relative to weight show high variability in terrestrial snails and slugs (from 0.491 to 1.394;

Rollo, 1988). In contrast, the b-values (0.69 and 0.72) for the two freshwater gastropods listed by Rollo (1988) were close to the value obtained here for LC-LW ($b = 0.651$). Perhaps the higher variation in the relative ingestion rates of terrestrial mollusks is related to their marked daily rhythms of activity and to feeding opportunities that vary in an unpredictable way according to weather conditions. When food supplies are constant, *P. canaliculata* apparently feeds quite continuously both during the day and night (Estebenet & Martín, 2002; pers. obs.), although the activity level is higher during dark hours (Heiler et al., 2008). Jeschke & Tollrian (2005) observed that feeding times for the rams-horn apple snail *Marisa cornuarietis* (Linnaeus, 1758) are exceptionally high relative to those of a heterogeneous array of herbivores.

In our study, the amount of lettuce consumed increased quadratically ($b = 1.932$) for snails between 5 and 55 mm of shell length. Cazzaniga (1981) found that absolute ingestion rates for *P. canaliculata* snails feeding on *Chara vulgaris* increase monotonically between 42.5 and 62.5 mm of shell length but decreased for bigger snails (up to 72.5 mm). Due to the asymptotic growth pattern of this species (Estebenet & Martín, 2002), it is likely that the largest snails were disproportionately older and consequently already reaching senescence.

Females of *P. canaliculata* had a specific ingestion rate that was 50% higher than that of males. This could be related to the relatively smaller mid-gut gland of the males (61–72% of that of females; Vega et al., 2006), in which a greater portion of the visceral mass is occupied by the gonad, probably imposing a restriction in the amount of food that can be processed by unit time.

In our study, the males of *P. canaliculata* showed lower growth efficiencies than females, probably resulting from a higher waste of undigested food related to their smaller mid-gut gland, which in turn results in lower food assimilation. An alternative explanation would be a smaller fraction of assimilated resources devoted to growth in males (e.g., due to higher basal metabolic rates or to higher activity rates). However, this seems unlikely since specific oxygen consumption rates showed no intersexual differences in other *Pomacea* spp. (Freiburg & Hazelwood, 1977; Santos & Mendes, 1981), and in the particular case of *P. canaliculata* no sexual differences have been recorded in the lung ventilation frequency (Seuffert & Martín, 2009). It is worth mentioning that the mid-gut

gland of females of *P. canaliculata* contains a 2.4-times higher concentration of a putative cyanobacterial endocytobiont than that of males (Koch et al., 2006; Vega et al., 2006), although their eco-physiological significance is far from being understood (secretion of proteases has been suggested; Godoy et al., 2005).

Even during pre-reproductive life, conversion efficiencies (FCE) were higher in females than in males, mostly due to its earlier decrease in the latter, especially at high food availabilities. Again, this could be explained by the smaller mid-gut gland of males owing to a greater portion of the visceral mass being taken up by the gonad (Vega et al., 2006). Coincidentally, in most males at the highest FA% levels (100–47%), the testicle was already observable through the shell by the second week of the experiment, while in those of the lowest levels (FA33–20%), the testicles were detected only at the fourth week and were clearly smaller (Tamburi & Martín, 2009).

The decrease in conversion efficiencies (FCE) along Experiment 2 was more important and earlier at high food availability levels. This generalized decline could be explained by the ageing of snails, by allometric limitations with size increase, or by the combination of both processes during growth. Ageing does not seem to be the main cause, since the efficiencies (AFC) estimated at the same size were the same across the different food availability levels, which differed greatly in the age necessary to attain a given shell length (Figs. 7, 8; Tamburi & Martín, 2009). The higher efficiencies (FCE) of snails under low food availabilities is probably due to the fact that they remain small and hence there is a lower decrease in the area of food absorption relative to the volume that must be nourished. However, the influence under deprived conditions of a higher absorption rate (e.g., due to higher retention times in the gut) or an increase in autocoprophagy cannot be ruled out. Haniffa (1982) found that absorption efficiencies in *P. globosa* also decreased with food availability.

Conversion efficiencies (FCE) for *P. globosa* (estimated from absorption and net conversion efficiencies in Table 1 in Haniffa (1982)) showed no effect of food availability and size on the range of food availabilities at which snails were able to grow. Food conversion rates (FCR, the inverse of our FCE) in *Pomacea bridgesii* (Reeve, 1856) were not affected by feeding levels ranging from 2% to 6% of snail live weight and a slightly higher efficiency was detected in small snails (Mendoza et al., 1999); food

conversion rates in this study decreased with food crude protein contents ranging between 15% and 40% but Ramnarine (2004) found no such effect for *Pomacea urceus* (Müller, 1774) within the same range. Rearing *P. canaliculata* snails on a paper diet for 60 days reduces the mass of the mid-gut gland of males and females relative to those fed on a mixed diet (Vega et al., 2005), and this could affect their efficiency. Apparently size and food quality are important in determining food conversion efficiencies in apple snails but feeding level is not; the influence of sex, another important factor according to our results, has not been considered in previous studies.

The possibility of sexual dimorphism in feeding rates has not been considered in recent studies dealing with the subject in *P. canaliculata* and *P. insularum* (e.g., Peña & Pocsidio, 2007; Boland et al., 2008; Burlakova et al., 2009). Even if the sex ratio is balanced, the random sampling of snails to be subjected to different treatments can result in biased sex ratios in them, especially if samples are small; the sexually dimorphic feeding rates can greatly increase the variability of estimations or bias the means of certain treatments. The highly biased sex ratios reported in *P. canaliculata* egg masses and families (Yusa, 2007) can confound inter-study comparisons if sex ratio is not portrayed in the results.

Carlsson & Brönmark (2006) demonstrated that small *P. canaliculata* snails have higher foraging abilities than large ones, a conclusion strongly supported by our results, and suggested that this may also explain, through resource depletion, their higher competitive ability in terms of size increase. Our results indicate that size-dependent efficiency can also play a role in the competitive dynamics of *P. canaliculata* populations. Grazing would be more intense, and at the same time more selective (Carlsson & Brönmark, 2006), during the recruitment period, a fact that could affect macrophyte replacement or depletion (Tamburi & Martín, 2009), depending on the phenological cycle of palatable and unpalatable macrophytes in each waterbody.

According to our data, 103 newborn snails (5 mm long) would consume the same amount of lettuce, or vegetation, as one mature snail 55 mm long. One female can lay dozens of egg-masses composed of hundreds of eggs in one reproductive season (Estebenet & Martín, 2002; Martín & Estebenet, 2002), and at the end of it small snails comprise the majority of population in paddy fields (Wada & Matsukura,

2007). This strongly supports the predictions of Carlsson & Brönmark (2006) and Boland et al. (2008) that small snails, albeit inconspicuous, can be responsible as a group for a great part of the damage caused by apple snails in aquatic crops and natural wetlands, at least during the reproductive season.

The males of *P. canaliculata* have been shown to have lower growth rates than females (Estebenet & Cazzaniga, 1998; Tanaka et al., 1999; Estebenet & Martín, 2002; Estoy et al., 2002; Martín & Estebenet, 2002; Tamburi & Martín, 2009), and in this study they also exhibit lower ingestion rates and growth efficiencies relative to females. Size at maturity is very much less plastic than age at maturity in females, whereas the opposite is true in males (Tamburi & Martín, 2009). Male size is not relevant to the probability of copulation (Estebenet & Martín, 2002; Estoy et al., 2002) and has no effect on female reproductive output (Tamburi & Martín, 2009); in contrast, female size at maturity seems to be constrained by their high reproductive costs and the need to produce big, highly elaborate egg masses (Estoy et al., 2002; Tamburi & Martín, 2009). Consequently, a selection pressure to maximize growth rates would be expected in females, while this trait is unimportant in males. In males, the main pressure is probably to copulate as soon, and with as many females, as possible and to maximize the sperm transferred during each copulation, in order to have an advantage in sperm competition inside the female genitalia (Yusa, 2004; Burela & Martín, 2007). This probably means an increase in testicle size, which in turn reduces the mid-gut gland size and its capacity to process food, growth rate being reduced just as a by-product of the maximization of sperm production though probably without a collateral reduction in overall male fitness.

Contrary to many invertebrates (mostly arthropods) and other mollusks the energetic reserves of gastropod's embryos are located in the perivitelline fluid that surrounds egg-cell and not in the egg-cell itself (Heras et al., 1998, 2007). In the case of *P. canaliculata*, there seems to be a strong competition for space within the visceral mass between the food digestion-assimilation and the reproductive functions. In females, the organs that provide the eggs with the necessary reserves and protective structures (Catalán et al., 2002, 2006) cannot be accommodated inside the visceral mass without detriment to the digestive-assimilative functions performed by the mid-gut gland. This constraint has probably promoted

the progressive assignment of these functions to the parts of the oviduct located outside the visceral mass, a trend that is widespread among gastropods (Fretter, 1984; Geraerts & Joose, 1984; Barker, 2001).

Our growth efficiencies results on *P. canaliculata*, albeit covering only the pre-reproductive phase, explain in part why females tend to grow to be larger than males (Estebenet & Cazzaniga, 1998; Estoy et al., 2002; Estebenet & Martín, 2003). The energetic budget probably changes at maturity for both sexes (Eleutheriadis & Lazaridou-Dimitriadou, 1995), but apparently not enough to hide the dimorphic pattern already expressed, which is probably due to the asymptotic decline in growth rates during their lifetime. This pattern is probably reinforced by the fact that after the beginning of testicular growth, males show a lower ingestion rate than females, and this is maintained during the reproductive lifespan. Bigger female sizes have also been reported for other species of ampullariids (Demian & Ibrahim, 1972; Burky, 1974; Keawjam, 1987; Lum-Kong & Kenny, 1989; Perera & Walls, 1996). Considering that testicle size and its occupancy of the visceral mass are higher than that of the ovary in most apple snails (except perhaps in *Afropomus balanoideus* (Gould, 1850); Berthold, 1988, 1989; Cowie et al., 2006), it is feasible that dimorphic ingestion rates and growth efficiencies are the cause of this widespread dimorphic pattern.

ACKNOWLEDGEMENTS

This work was funded with grants by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET; PIP 6150) and Universidad Nacional del Sur (PGI 24/B108). NET is a doctoral fellow and PRM a researcher in CONICET.

LITERATURE CITED

- BARKER, G. M., 2001, Gastropods on land: phylogeny, diversity and adaptive morphology. Pp: 1–146, in: G. M. BARKER, ed., *The biology of terrestrial molluscs*. Landcare Research, Hamilton, New Zealand, xix + 558 pp.
- BELOVSKY, G. E., J. FRYXELL & O. J. SCHMITZ, 1999, Natural selection and herbivore nutrition: optimal foraging theory and what it tells us about the structure of ecological communities. Pp. 1–70, in: H.-J. G. JUNG & G. C. FAHEY, JR., eds. *Nutritional ecology of herbivores: Proceedings of the Vth International Symposium on the Nutrition of Herbivores*. American Society of Animal Science, Savoy, Illinois, 836 pp.
- BERTHOLD, T., 1988, Anatomy of *Afropomus balanoideus* (Mollusca, Gastropoda, Ampullariidae) and its implications for phylogeny and ecology. *Zoomorphology*, 108: 149–159.
- BERTHOLD, T., 1989, Comparative conchology and functional morphology of the copulatory organ of the Ampullariidae (Gastropoda, Monotocardia) and their bearing upon phylogeny and palaeontology. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, NF, 28: 141–164.
- BOLAND, B. B., M. MEERHOFF, C. FOSALBA, N. MAZZEO, M. A. BARNES & R. L. BURKS, 2008, Juvenile snails, adult appetites: contrasting resource consumption between two species of applesnails (*Pomacea*). *Journal of Molluscan Studies*, 74: 47–54.
- BURELA, S. & P. R. MARTÍN, 2007, Nuptial feeding in the freshwater snail *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Malacologia*, 49: 465–470.
- BURKY, A. J., 1974, Growth and biomass production of an amphibious snail, *Pomacea urceus* (Müller), from the Venezuelan savannah. *Proceedings of the Malacological Society of London*, 41: 127–143.
- BURLAKOVA, L. E., A. Y. KARATAYEV, D. K. PADILLA, L. D. CARTWRIGHT & D. N. HOLLAS, 2009, Wetland restoration and invasive species: apple snail (*Pomacea insularum*) feeding on native and invasive aquatic plants. *Restoration Ecology*, 17: 433–440.
- CARLSSON, N. O. L. & C. BRÖNMARK, 2006, Size-dependent effects of an invasive herbivorous snail (*Pomacea canaliculata*) on macrophytes and periphyton in Asian wetlands. *Freshwater Biology*, 51: 695–704.
- CARLSSON, N. O. L., C. BRÖNMARK & L.-A. HANSSON, 2004, Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology*, 85: 1575–1580.
- CATALÁN, N. M. Y., S. N. FERNÁNDEZ & B. C. WINIK, 2002, Oviductal structure and provision of egg envelopes in the apple snail *Pomacea canaliculata* (Gastropoda, Prosobranchia, Ampullariidae). *Biocell*, 26: 91–100.
- CATALÁN, N. M. Y., M. S. DREON, H. HERAS, R. J. POLLERO, S. N. FERNÁNDEZ & B. WINIK, 2006, The pallial oviduct of *Pomacea canaliculata* (Gastropoda): ultrastructural studies of the parenchymal cellular types involved in the metabolism of perivitellins. *Cell and Tissue Research*, 324: 523–533.
- CAZZANIGA, N. J., 1981, Evaluación preliminar de un gasterópodo para el control de malezas acuáticas sumergidas. Pp. 131–163, in: CIC ed., *II Reunión sobre malezas subacuáticas en canales de desagüe de CORFO*, CIC, La Plata, 168 pp.
- COWIE, R. H., 2002, Apple snails (Ampullariidae) as agricultural pests: Their biology, impacts and management. Pp. 145–192, in: G. M. BARKER, ed., *Molluscs as crop pests*. CABI Publishing, Wallingford, 468 pp.

- COWIE, R. H., K. A. HAYES & S. C. THIENGO, 2006, What are apple snails? Confused taxonomy and some preliminary resolution. Pp. 3–23, in: R. C. JOSHI & L. S. SEBASTIAN, eds., *Global advances in ecology and management of golden apple snails*. Philippine Rice Research Institute, Nueva Ecija, 600 pp.
- DEMIAN, E. S. & A. M. IBRAHIM, 1972, Sexual dimorphism and sex ratio in the snail *Marisa cornuarietis*. *Bulletin of Zoological Society of Egypt*, 24: 52–63.
- ELEUTHERIADIS, N. & M. LAZARIDOU-DIMITRIDOU, 1995, Age-related differential catabolism in the snail *Bithynia graeca* (Westerlund, 1879) and its significance in the bioenergetics of sexual dimorphism. *Malacologia*, 36: 139–146.
- ESTEBENET, A. L. & N. J. CAZZANIGA, 1998, Sex-related differential growth in *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Journal of Molluscan Studies*, 64: 119–123.
- ESTEBENET, A. L. & P. R. MARTÍN, 2002, *Pomacea canaliculata* (Gastropoda: Ampullariidae): life-history traits and their plasticity. *Biocell*, 26: 83–89.
- ESTEBENET, A. L. & P. R. MARTÍN, 2003, Shell interpopulation variation and its origin in *Pomacea canaliculata* (Gastropoda: Ampullariidae) from southern Pampas Argentina. *Journal of Molluscan Studies*, 69: 301–310.
- ESTEBENET, A. L., P. R. MARTÍN & S. BURELA, 2006, Conchological variation in *Pomacea canaliculata* and other South American Ampullariidae (Caenogastropoda, Architaenioglossa). *Biocell*, 30: 329–335.
- ESTOY, G. F., Y. YUSA, T. WADA, H. SAKURAI & K. TSUCHIDA, 2002, Effect of food availability and age on the reproductive effort of the apple snail, *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Applied Entomology and Zoology*, 37: 543–550.
- FREIBURG, M. W. & D. H. HAZELWOOD, 1977, Oxygen consumption of two amphibious snails: *Pomacea paludosa* and *Marisa cornuarietis* (Prosobranchia: Ampullariidae). *Malacologia*, 16: 541–548.
- FRETTER, V., 1984, Prosobranchs. Pp. 1–45, in: K. M. WILBUR, ed., *The Mollusca*, Vol. 7: *Reproduction*. Academic Press, New York, xix + 486 pp.
- GERAERTS, W. P. M. & J. JOOSE, 1984, Freshwater Snails (Basommatophora). Pp. 141–207, in: K. M. WILBUR, ed., *The Mollusca*, Vol. 7: *Reproduction*. Academic Press, New York, xix + 486 pp.
- GODOY, S. M., I. A. VEGA & A. CASTRO-VAZQUEZ, 2005, Is there any protease activity in the digestive system of the apple-snail *Pomacea canaliculata*? *Biocell*, 29: 364.
- HANNIFA, M. A., 1982, Effects of feeding level and body size on food utilization of the freshwater snail *Pila globosa*. *Hydrobiologia*, 97: 141–149.
- HAYES, K. A., R. C. JOSHI, S. C. THIENGO & R. H. COWIE, 2008, Out of South America: multiple origins of non-native apple snails in Asia. *Diversity and Distributions*, 14: 701–712.
- HERAS, H., C. GARÍN & R. POLLERO, 1998, Biochemical composition and energy source during embryo development and in early juveniles of the snail *Pomacea canaliculata* (Mollusca: Gastropoda). *Journal of Experimental Zoology*, 280: 375–383.
- HERAS, H., M. S. DREON, S. ITUARTE & R. J. POLLERO, 2007, Egg carotenoproteins in neotropical Ampullariidae (Gastropoda: Architaenioglossa). *Comparative Biochemistry and Physiology, C – Toxicology and Pharmacology*, 146: 158–167.
- HEILER, K. C. M., P. V. VON OHEIMB, K. EKSCHMITT & C. ALBRECHT, 2008, Studies on the temperature dependence of activity and on the diurnal activity rhythm of the invasive *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Mollusca*, 26: 73–81.
- JESCHKE, M. & R. TOLLRIAN, 2005, Predicting herbivore feeding times. *Ethology*, 111: 187–206.
- JOSHI, R. C. & L. S. SEBASTIAN, 2006, *Global advances in ecology and management of golden apple snails*. Philippine Rice Research Institute, Nueva Ecija, 600 pp.
- KEAWJAM, R. S., 1987, The apple snails of Thailand: aspects of comparative anatomy. *Malacological Review*, 20: 69–90.
- KOCH, E., I. A. VEGA, E. A. ALBRECHT, H. H. ORTEGA & A. CASTRO-VAZQUEZ, 2006, A light and electron microscopic study of pigmented corpuscles in the midgut gland and feces of *Pomacea canaliculata* (Caenogastropoda: Ampullariidae). *The Veliger*, 48: 17–25.
- LOWE, S., M. BROWNE, S. BOUDJELAS & M. DE POORTER, 2000, *100 of the World's Worst Invasive Alien Species*. The Invasive Species Specialist Group, IUCN, Auckland, 12 pp.
- LUM-KONG, A. & J. S. KENNY, 1989, The reproductive biology of the ampullariid snail *Pomacea urceus* (Müller). *Journal of Molluscan Studies*, 55: 53–66.
- MARTÍN, P. R. & A. L. ESTEBENET, 2002, Interpopulation variation in life-history traits of *Pomacea canaliculata* (Gastropoda: Ampullariidae) in Southwestern Buenos Aires Province, Argentina. *Malacologia*, 44: 153–163.
- MENDOZA, R., C. AGUILERA, J. MONTEMAYOR & G. RODRÍGUEZ, 1999, Utilization of artificial diets and effect of protein/energy relationship on growth performance of the apple snail *Pomacea bridgesi* (Prosobranchia: Ampullariidae). *The Veliger*, 42: 109–119.
- PEÑA, S. & G. POCSIDIO, 2007, Influence of copper on the feeding rate, growth and reproduction of the Golden Apple Snail, *Pomacea canaliculata* Lamarck. *Bulletin of Environmental Contamination and Toxicology*, 79: 606–608.
- PERERA, G. & G. H. WALLS, 1996, *Apple snails in the aquarium*. T.F.H. Publications, Neptune City, 121 pp.
- RAMNARINE, I. W., 2004, Quantitative protein requirements of the edible snail *Pomacea urceus* (Müller). *Journal of the World Aquaculture Society*, 35: 253–256.
- RAWLINGS, T. A., K. A. HAYES, R. H. COWIE & T. M. COLLINS, 2007, The identity, distribution,

- and impacts of non-native apple snails in the continental United States. *BMC Evolutionary Biology*, 7: 97–111.
- ROLLO, C. D., 1988, A quantitative analysis of food consumption for the terrestrial mollusca: allometry, food hydration and temperature. *Malacologia*, 28: 41–51.
- SANTOS, C. A. Z. & E. G. MENDES, 1981, Oxygen consumption of the amphibious snail *Pomacea lineata*: influence of weight, sex and environments. *Comparative Biochemistry and Physiology*, 86: 595–598.
- SANTOS, C. A. Z., C. H. S. PENTEADO & E. G. MENDES, 1987, The respiratory responses of an amphibious snail *Pomacea lineata* (Spix, 1827), to temperature and oxygen tension variations. *Comparative Biochemistry and Physiology*, 86: 409–415.
- SEUFFERT, M. E. & P. R. MARTÍN, 2009, Influence of temperature, size and sex on aerial respiration of on *Pomacea canaliculata* (Gastropoda: Ampullariidae) from southern Pampas, Argentina. *Malacologia*, 51: 191–200.
- STAMPS, J. A. & V. V. KRISHNAN, 1997, Sexual bimaturation and sexual size dimorphism in animals with asymptotic growth after maturity. *Evolutionary Ecology*, 11: 21–39.
- TAKEDA, N., 1999, Histological studies on the maturation of the reproductive system in the apple snail, *Pomacea canaliculata*. *Journal of Analytical Biosciences*, 22: 425–432.
- TAMBURI, N. E. & P. R. MARTÍN, 2009, Reaction norms of size and age at maturity of *Pomacea canaliculata* (Gastropoda: Ampullariidae) under a gradient of food deprivation. *Journal of Molluscan Studies*, 75: 19–26.
- TANAKA, K., T. WATANABE, H. HIGUCHI, K. MIYAMOTO, Y. YUSA, T. KIYONAGA, H. KIYOTA, Y. SUZUKI & T. WADA, 1999, Density dependent growth and reproduction of the apple snail, *Pomacea canaliculata*: a density manipulation experiment in a paddy field. *Research in Population Ecology*, 41: 253–262.
- VEGA, I. A., M. C. DAMBORENEA, C. GAMARRALUQUES, E. KOCH, J. A. CUETO & A. CASTRO-VAZQUEZ, 2006, Facultative and obligate symbiotic associations of *Pomacea canaliculata* (Caenogastropoda, Ampullariidae). *Biocell*, 30: 367–375.
- YUSA, Y., 2004, Inheritance of colour polymorphism and the pattern of sperm competition in the apple snail *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Journal of Molluscan Studies*, 70: 43–48.
- YUSA, Y., 2007, Nuclear sex-determining genes cause large sex-ratio variation in the apple snail *Pomacea canaliculata*. *Genetics*, 175: 179–184.
- YUSA, Y., N. SUGIURA & T. WADA, 2006, Predatory potential of freshwater animals on an invasive agricultural pest, the apple snail *Pomacea canaliculata* (Gastropoda: Ampullariidae), in southern Japan. *Biological Invasions*, 8: 137–147.
- WADA, T. & K. MATSUKURA, 2007, Seasonal changes in cold hardiness of the invasive freshwater apple snail, *Pomacea canaliculata* (Lamarck) (Gastropoda: Ampullariidae). *Malacologia*, 49: 383–392.

Revised ms. accepted 15 December 2008